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Inheritance of bacterial leaf blight resistance in crosses involving inter-specific and intra-specific rice genotypes

Lussewa RK[1], Edema R[2], Gibson P[2], Lamo J[3]

[1]Agricultural Research Institute-Ukirigurox 1433, Mwanza, Tanzania;
[2]Department of Agricultural Production, Makerere University, Uganda
[3]Namulonge National Crop Resource Research Institute, Kampala, Uganda

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ABSTRACT

Bacterial leaf blight (BLB) of rice, caused by *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) is one of the oldest known disease which was first reported by farmers of Japan in 1884. Subsequently, its incidence has been reported from different parts of Asia, northern Australia, Africa, and the USA and has become one of the three serious rice diseases. In Africa, BLB was first identified in the 1980s and has continued to increase in importance. It characterized by a high degree of race-cultivar specificity. It is a serious problem under irrigated and high fertilizer input conditions which are conducive for disease development. BLB causes reductions in crop yields as high as up to 80% and deterioration of grain quality under severe epidemics. In Uganda apart from being reported as early as 2003, some strains were also reported to affect rice in Kibimba and Eastern Uganda back in 2010. Attempts to control this disease through the use of chemicals are not cost effective and environmental friendly for resource constraint farmers. Use of resistant varieties is considered the only viable option. The effort to determine the inheritance of BLB 2011 in Uganda involved crossing of four BLB resistant genotypes, namely NERICA1, NERICA4, CT12 and IR09A to five susceptible and locally preferred cultivars: K85, K5,

GSR-I-0057, CT 145 and IR24. The F_2 were then inoculated with one BLB isolate-UG 20-2, most virulent in laboratory testing out of 20 BLB isolated from four regions of Uganda. Results has shown highly significant differences among genotypes at $P<0.001$. The GCA effects revealed that parents NERICA1, NERICA 4, CT 12 and IR 09A were good general combiners, showing that they can be utilized in future rice breeding cultivars with resistance to BLB. Reciprocal effects were also significant at $P<0.01$, indicating that maternal gene effects had a contribution to the modification of genotypic resistance to BLB. It was also revealed that IR 24, which is used as a universal susceptible check in Asian rice populations, showed partial resistance indicating the presence of one or more genes conferring resistance to the Ugandan BLB isolate. This indicates that the isolates in Uganda are different from those in Asia. The predominance of GCA effects (Baker's ratio = 75%) over SCA suggests that additive genetic effects are more important than non-additive in the inheritance of resistance in the genotypes evaluation. The values for narrow sense coefficient of genetic determination (NSCGD) and broad sense coefficient of genetic determination (BSCGD) were also very high (57% and 77%, respectively).

Key words: Inheritance, bacterial leaf blight, interspecific, intraspecific, rice, Uganda

1. INTRODUCTION

Rice (*Oryza sativa*) is the world's most important food, being a major source of calories and protein to more than half of the world's population, and accounts for 25% of global caloric intake (Fairfood Intern. 2011). It provides nutrition for more people in the world than does any other crop, especially in developing countries (Phillips *et al.* 2005). The importance of rice is increasingly becoming a regular food for many families and communities in Sub- Saharan Africa (SSA) (FAOSTAT, 2008). Globally, rice, wheat, and maize are the three leading cereal food crops directly supplying more than 50% of calories consumed by the entire human population. Eighty five percent of rice produced, is used for human consumption, compared to 72% of wheat and 19% of maize (IRRI, 2006). Rice provides 21% of global human per capita energy and 15% of per-capita protein. Although rice protein ranks high in nutritional quality among cereals, its protein content is modest (FAO, 2001). The world average consumption of rice in 1999 was 58 kg, with the highest intake in some Asian countries (FAO, 2002); Myanmar has the highest annual consumption at 211 kg/person (FAO 2003).
Initiatives aimed at promoting local rice production where conditions are favorable, are considered viable strategies to avoid competition for this commodity. Rice is also recognized as a crop that can feed large populations based on several of its attributes, including good storability and easy to prepare.

In Uganda rice is cultivated under three production systems: upland (60%), rain-fed lowland (36%) and irrigated wetland (4%), with each system contributing 40%, 42% and 18%, respectively, of the total rice produced in the country (JICA, 2007). These production systems have changed in emphasis over time. Rain-fed lowland production was the main ecosystem from 1904 to 1970, followed by irrigated rice production during 1971 to 1995period and upland rice has been cultivated most extensively from1995 to date (Odogoola, 2006; JICA, 2007).

A common denominator in the three production systems is that, there is high potential for rice production. About 70% of the country's arable land is suitable for rain-fed upland rice production (Ogwang, 2002; JICA, 2007). Recently, there has been a steady increase in the rice area, -from 86,000 ha to 119,000 ha in 2003 to 2007(FAOSTAT, 2008). However, during that time the average yield had declined from 1.5 t ha-1 to 1.4 t ha-1 and the annual consumption has grown steadily from 5 kg to 8.3 kg in 2008 (FAOSTAT, 2008). It is projected to increase to 15.6 kg by 2017, making the total consumption high in light of the current population growth rate of 3.2% (UNFPA, 2008).

Despite the growing importance of rice, biotic stresses severely affect its yields in the region,with diseases being considered the most important (Séré *et al.* 2009; Onasanya *et al.* 2010). The major rice disease of economic threats in East Africa include rice blast (*Pyricularia oryzae*), rice yellow mottle virus and bacterial leaf blight (*Xanthomonas oryzae* pv. *oryzae*) (Yamamoto *et al.* 1995; Séré *et al*. 2005; Onasanya *et al*. 2010).

Little attention has been given to bacterial leaf blight (BLB), partly because of the difficulty in differentiating it from other foliar diseases and lack of information on the yield loss associated with it (Séré *et al.* 2012 per.comm). Recent studies show that BLB is a very destructive disease in Africa, and its control is a bit difficulty (Séré *et al*. 2005). In Uganda, the disease was first reported in 2003 (Biruma, *et al.* 2003), and in 2010, the destructive strains *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) 2 and *Xoo* 4 were reported (Onasanya *et al*. 2010). These two strains devastated all popular local varieties including K5 and K85 (Onasanya *et al*. 2010). As a result, farmers abandoned these varieties due to their high susceptibility to BLB and other foliar diseases (Onasanya *et al.* 2010).

Bacterial leaf blight in rice has rendered useless the high yielding characteristics and farmer-preferred quality traits that were

incorporated into Uganda's locally adapted varieties (Dr. Jimmy Lamo, 2011 per.comm.). BLB also complicates variety screening because several introductions from East Africa region and elsewhere have succumbed to the disease (Onasanya *et al.* 2010). In Tanzania, BLB has been reported in most rice growing areas, where rice is important cereal crop, (Yamamoto *et al.* 1995). The yield loss to BLB ranges from 10-100%, depending on the cultivar, location and the type of disease (Kanyeka, *et al.* 2007; Luzi-Kihupi, 2001).

2. MATERIAL AND METHOD

2.1. Experimental site

A crossing block was established and maintained in a screen house at the National Crops Resources Research Institute (NaCRRI)-Namulonge. Namulonge, is located at 0º 31' 47" N and 32º 36' 9" E at an elevation of 1,133 meters above sea level. It has a bimodal type of rainfall with an annual mean rainfall of 1,300 mm, with the first rain season from April to July and the second season in September to December. The site has a tropical wet and a mild dry climate with slightly humid conditions averaging 65% humidity. Temperatures rarely rise beyond 28^0C, with the minimum about 15^0C, and typically less than 70% relative humidity (Lugojja *et al.* 2002; NARO, 2005)

2.2. Experimental design

2.2.1. Development of breeding populations

A North Carolina II (NC2) mating design with reciprocal crosses was used. The design was selected because information on the reaction of the selected parents was already known. Four resistant rice genotypes were crossed with five susceptible parents. Each of the parents was sown in separate germination buckets. Planting of each parent was staggered for 7-days intervals to synchronize flowering between the male and female parents. Planting started in the first week of March 2011. A modified vacuum emasculator was used to thoroughly remove the anthers as described by Coffman and Herera, (1980) and Lamo, (2010). The emasculated panicles were covered with paper bags to protect their stigmas from desiccation or being naturally pollinated by unwanted pollen. After emasculation,the female plants were carefully watered.

To ensure only true crosses were advanced, the F_1 plants were carefully inspected for presence of selfed-progenies before and after flowering. Plants that were not true crosses were identified by their expression of simply inherited morphological characters that are known to be inherited through dominant genes, such as base culm colour, presence of awn, plant height of the different parents and stigma colour (Lamo, 2010).

The F_1 seeds were harvested at maturity when the seeds had lost their green colour, about 21-25 days after pollination (Navarro and Virmani, 1987). This was done by cutting the panicles followed by drying and threshing. Glume remnants were removed and the F_1 seeds from each cross counted kept in well-labeled envelopes. The F_1 populations were advanced to F_2 between November 2011 and February 2012. The numbers of seeds germinated from every cross were recorded.

To enhance production of adequate F_2 seed, NPK fertilizer (40 + 50 + 50 kg/ha) was applied as a basal-dressing on the day of transplanting. Top-dressing with 40 kg/ha N was done at 35 days after transplanting. Pots were kept weed-free, although no chemical control against insect pests or disease was carried out.

2.2.2. Collection of BLB isolates and inoculum preparation

The isolates of *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) were isolated from diseased leaves samples collected from four regions of Uganda in 10 locations, known to have the disease (Onasanya *et al.* 2010). Two diseased samples were collected from each location (Table 4).

Table 1 Bacterial leaf disease samples collected from four regions in Uganda

Location	Isolate code	Region	Host variety	%Disease Incidence	GPS coordinates	
Namulonge	UG1 &UG2	Central	NERICA10	75	N 0^0 31'42.6"	E 32^0 37' 37.2"
Masindi	UG3 & UG4	Western	NERICA1	45	N 1^0 48' 13"	E 31^0 59' 50"
Lira	UG5 & UG6	North	Supa	70	N 2^0 11' 49.3"	E 33^0 1' 33.3"
Nakaloma	UG7 & UG8	Eastern	Local	65	N 0^0 30' 26.9"	E 33^0 30' 26.9"
Gogero	UG9 & UG10	Eastern	Local	65	N 0^0 36' 41.5"	E 33^0 40' 6.4"
Bugasere	UG11 & UG12	Eastern	Local	40	N 0^0 31' 29.9"	E 33^0 50' 22.8"

Doho	UG13 & UG14	Eastern	Local	55	N 0^0 56' 13.4"	E 34^0 0' 14.9"
Budaka	UG15 & UG16	Eastern	Local	45	N 1^0 0' 47.4"	E 34^0 55' 42.6"
Kibuku	UG17 & UG18	Eastern	Local	65	N 3^0 0' 10.7"	E 33^0 47' 32.1"
Limoto, Palisa	UG19 & UG20	Eastern	Local	60	N 1^0 6' 19.1"	E 33^0 44' 39.2"

2.2.3. Selection of pure isolate for F_2 evaluation

Five of the 20 isolates tested were found to be most virulent based on the laboratory results. These five pure isolates were then evaluated to select the most virulent using susceptible variety K5 as a check. The plants were planted in a randomized complete block design (RCBD) with three replications. Evaluation of the isolates was done in the screen- house conditions at NaCRRI-Namulonge. The most virulent isolate on K5 selected for inoculating the developed F_2 populations, was UG 20-2 from Limoto, Palisa.

2.2.4. Evaluation of parents and F_2 families

In an alpha-lattice design with 2 replications, 27 F_2 families (crosses and their reciprocals) and nine (9) parents were planted in a 5 x 10-arrangement of alpha–lattice design. These were sown in mini-paddy nurseries before being transplanted 15 days after emergence in well prepared plot in a screen house, with one seedling per hill at a spacing of 20cm x 12.5cm (i.e.40 plants per m^2).

Inoculation with the BLB isolate was done 21 days after transplanting. The clipping and spraying method was used to inoculate the plants (Kauffman *et al.* 1973). The inoculation was conducted in the evening and the inoculated leaves immediately were covered with a polyethylene bag and left overnight (Liu *et al.* 2007; Akhtar *et al*. 2008). Disease scoring was conducted 21 days after inoculation (DAI), by measuring the length of BLB lesions on each inoculated leaf (Yang *et al.* 2003; Gonzalez *et al.* 2007). Disease lesions were scored on three (3) leaves per hill (sub plot) and the average of these leaves provided the score for that sub plot. As described by Deng *et al.*(2006), plants with lesion lengths of less than 3 cms were regarded as resistant while plants with lesion lenghts of more than 3 cms were regarded as susceptible.

2.3. Data collection and analysis

2.3.1. Determination of number of genes controlling resistance to rice bacterial blight

The number of resistant or susceptible plants observed among 24 plants was counted and recorded based on Cottyn and Mew classification (2004) for each of the 27 F_2 progenies and 9 parents. For genetic analysis, resistant and moderately resistant plants were grouped together as resistant, while moderately susceptible and susceptible plants were grouped together as susceptible. A Chi-square test (Clewer and Scarisbrick, 2001) was performed to examine the goodness-of-fit between the observed and expected ratio of resistance to susceptible F_2 plants at 0.05 probability level of significance and 1 degree of freedom (df). The following formula was used:

$$\chi^2 = \Sigma \frac{(o_i - e_i)^2}{e_i},$$

Where;

χ^2 is Chi-square,
Σ is summation,
o_i is observed score of i^{th} plant, and
e_i is expected score of i^{th} plant in different crosses.

2.3.2. Combining ability estimates for parents and crosses

Data were recorded on a plot basis (Table 2). Collected data were analyzed using the Restricted Maximum Likelihood (ReML) procedure of GENSTAT 14thEdition (VSN International Ltd. www.vsni.co.uk) to obtain genotype means. The genotype means were then used in further analysis in Genstat to obtain estimates of general combining ability (GCA), specific combining ability (SCA) and reciprocal effects (REC).The GCA and SCA variance components obtained from the expected mean squares were used to determine Baker's ratio (Baker,1978), broad-sense coefficient of genetic determination (BSCGD) and narrow-sense coefficient of genetic determination (NSCGD) as described by Hall, (2002); Li et al. (2004), and Adefris and Becker, (2005)

Table 2 Outline of the ReML analysis for NC2 design crosses, GCA, SCA and reciprocal effects for the response of rice genotypes to bacterial leaf blight

Source	df	SS	MS	F	Expected Mean Square	Var. comp
Replications	1					
Crosses	39				$\sigma^2e + 2\sigma^2_{crosses}$	
$^1GCA_N$	3				$\sigma^2e + 15\sigma_{2GCAN}$	
$^2GCA_A$	4				$\sigma^2e + 12\sigma^2_{GCAA}$	
SCA	14				$\sigma^2e + 3\sigma^2_{SCA}$	
Reciprocal	7				e	
Residual	28				σ^2e	

$^1GCA_N$ = General combining ability (for the non-adapted/BLB resistant parents); $^2GCA_A$ = General combining ability (for the adapted/BLB susceptible parents); SCA = Specific combining ability

3. RESULTS

Most of the collected samples from the sites indicated to be affected by the Xanthomonas oryzae pv oryzae as shown in Table 3.

Table 3 Laboratory results of the isolated diseased samples from 20 sites of Uganda

S/N	Location	Host variety	% Disease Incidence	GPS		Isolate Code	KOH	Gram	Selective Medium
1	Namulonge	NERICA10	75	N 0^0 31'42.6"	E 32^0 37' 37.2"	UG1-1	+	-	+
						UG1-2	_	-	+
2	Namulonge	NERICA10	75	N 0^0 31'42.6"	E 32^0 37' 37.2"	UG2-1	–	+	+
						UG2-2	_	+	+
3	Masindi	NERICA1	45	N 1^0 48' 13"	E 31^0 59' 50"	UG3-1	_	+	+
						UG3-2	_	+	+
4	Masindi	NERICA1	45	N 1^0 48' 13"	E 31^0 59' 50"	UG4-1			
						UG4-2			
5	Lira	SUPA	70	N 2^0 11' 49.3"	E 33^0 1' 33.3"	UG5-1	+	_	+
						UG5-2	+	_	
6	Lira	SUPA	70	N 2^0 11' 49.3"	E 33^0 1' 33.3"	UG6-1	_	+	
						UG6-2	_	+	+
7	Nakaloma-	Cultivated rice	65	N 0^0 30' 26.9"	E 33^0 30' 26.9"	UG7-1			
						UG7-2			
8	Nakaloma-	Cultivated rice	65	N 0^0 30' 26.9"	E 33^0 30' 26.9"	UG8-1	–	+	+
						UG8-2	_	+	+
9	Gogero -Ig	Cultivated rice	65	N 0^0 36' 41.5"	E 33^0 40' 6.4"	UG9-1	–	+	+
						UG9-2	_	+	+
10	Gogero -	Cultivated rice	65	N 0^0 36' 41.5"	E 33^0 40' 6.4"	UG10-1			+
						UG10-2			+
11	Bugosere B	Cultivated	40	N 0^0 31' 29.9"	E 33^0 50' 22.8"	UG11-1			
						UG11-2			

12	Bugosere	Cultivated rice	40	N 0^0 31' 29.9"	E 33^0 50' 22.8"	UG12-1	–	+	
						UG12-2	_	+	+
13	Doho	Cultivated rice	55	N 0^0 56' 13.4"	E 34^0 0' 14.9"	UG13-1	–	+	+
						UG13-2	_	+	_
14	Doho	Cultivated rice	55	N 0^0 56' 13.4"	E 34^0 0' 14.9"	UG14-1	–	+	–
						UG14-2	_	+	+
15	Budaka	Cultivated rice	45	N 1^0 0' 47.4"	E 34^0 55' 42.6"	UG15-1	–	+	+
						UG15-2	_	+	+
16	Budaka	Cultivated rice	45	N 1^0 0' 47.4"	E 34^0 55' 42.6"	UG16-1	NA	NA	NA
						UG16-2	NA	NA	NA
17	Kibuku	Cultivated rice	65	N 3^0 0' 10.7"	E 33^0 47' 32.1"	UG17-1	NA	NA	NA
						UG17-2	NA	NA	NA
18	Kibuku	Cultivated rice	65	N 3^0 0' 10.7"	E 33^0 47' 32.1"	UG18-1	–	+	+
						UG18-2	_	+	+
19	Limoto Palisa	Cultivated rice	60	N 1^0 6' 19.1"	E 33^0 44' 39.2"	UG19-1	–	+	+
						UG19-2	+	_	+
20	Limoto Palisa	Cultivated rice	60	N 1^0 6' 19.1"	E 33^0 44' 39.2"	UG20-1	–	+	–
						UG20-2	_	+	+

3.1. Virulence of pure BLB isolates tested against variety K5

The mean squares from the analysis of variance (ANOVA) revealed highly significant differences ($P \leq 0.001$) among the five isolates (Table 4).

Table 4 Mean squares of virulence of five BLB isolates on the genotype K5

Source of variation	d.f	m.s	v.r.	F pr.
Replication	2	0.152	3.02ns	
Isolates	4	0.892	17.73***	<.001
Residual	8	0.050		
Total	14			

ns: non-significant; ***: significant at $p \leq 0.001$

The most virulent isolate on rice variety K5 was isolate UG 20-2 (4.2 cm) from Limoto, Palisa (Table 5). This was followed by Lira (3.6cm) and Namulonge (3.0cm) respectively, whereas isolates from Doho (1.4 cm) were less effective in transmitting the disease. These areas with the exception of Doho are the ones which were used in the second study for testing genotypes across different locations.

Table 5 Mean lesion length of the five evaluated BLB isolates against K5 rice variety

Isolate code	Site of collection	GPS description		Mean lesion length (cm)
UG 1-3	Namulonge	N0°31′ 42.6″	E32°37′37.2′′	3.0
UG 3-1	Masindi	N1°48′13′′	E31°59′50′′	2.4
UG 5-1	Lira	N2°11′49.3′′	E33°1′33.3′′	3.6

UG 13-1	Doho	N0°56'13.4''	E34°0'14.9''	1.4
UG 20-2	Limoto-Palisa	N1°6'19.1''	E33°44'39.2''	4.2
Mean	-		-	2.92
F-prob.				< 0.001
LSD				0.422
CV (%)				15.4

***: significant at p ≤ 0.001

3.2. The mode of inheritance of BLB resistance trait in rice

3.2.1. Goodness-of-fit : the observed and expected ratios of resistant to susceptible F_2 plants

The basic segregation pattern of most crosses was continuous, which suggested a quantitative inheritance. However, because of the possibility that the experiment failed to separate distinctly the resistance and susceptible classes, an oligogenic interpretation was also attempted. Therefore a Chi-Square Test was performed on 12 F_2 crosses with 24 plants each to determine the goodness-of-fit based on the expected 3:1 phenotypic ratio. Results of the Chi-Square Analysis of the F_2 population indicated that the 24 progenies tested segregated in a wide range of response to isolate UG20-2 (Table 6). The segregation, grouped the crosses into three groups according to resistant : susceptible ratios. Group one was composed of 3 crosses; NERICA4 x K85, NERICA4 x K5 and GSR-I-0057x NERICA1, which fit 3:1 ratio. The second group had 6 crosses; NERICA1 x CT 145, K5 x CT12, NERICA4 x GSR-I-0057, NERICA1 x K85, CT12 x GSR-I-0057, CT12 x CT 145 which fit 13:3 ratio. The third group had 3 crosses, CT12 x K5, NERICA1 x GSR-I-0057, and IR096 x IR24 segregated in 15:1 ratio. Some crosses exhibited segregating patterns different from the corresponding reciprocal crosses and consequently fitted into multiple segregating ratios. For instance, GSR-I-0057x NERICA1 fit 3:1 and NERICA1 x GSR-I-0057 fit a 15:1 ratios. The severity distribution of the Xoo in some crosses has shown a wide range as in figure 1-4.

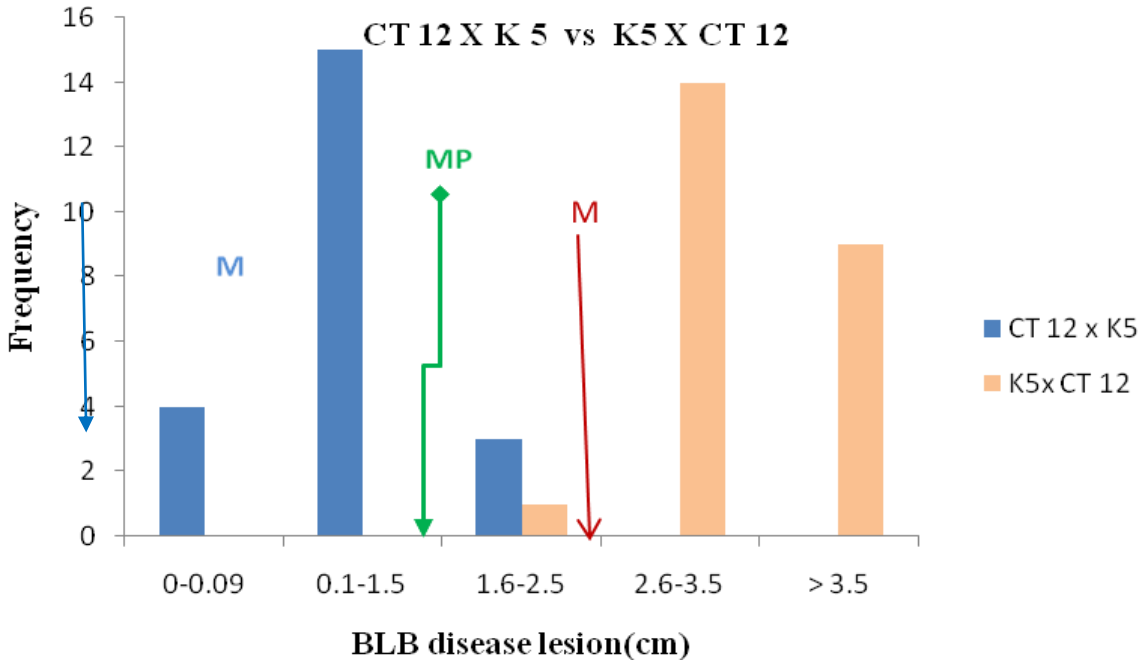

Figure 1 Frequency distribution for UGX20-2 severity in a cross CT12 x K5 and its reciprocal cross

Table 6 Chi-Square for segregation ratios of resistance: susceptibility against UG20-2 BLB isolate

Crosses	Progenies tested	Observed ratio R	S	Expected ratio (R:S)	χ^2
NERICA 4 x K85	24	17	7	3:1	0.222
NERICA 4 x K5	24	17	7	3:1	0.222
GSR-I-0057x NERICA1	24	17	7	3:1	0.222
NERICA1 x CT 145	24	19	5	13:3	0.068

K5 x CT 12	24	19	5	13:3	0.068
NERICA 4 x GSR-I-0057	24	20	4	13:3	0.068
NERICA1 x K85	24	21	3	13:3	0.615
CT12 x GSR-I-0057	24	21	3	13:3	0.615
CT12 x CT145	24	21	3	13:3	0.615
CT12 x K5	24	23	1	15:1	0.178
NERICA1 x GR-I-0057	24	22	2	15:1	0.178
IR096 x IR24	24	23	1	15:1	0.178
TOTAL	**288**	**240**	**48**	-	-

χ^2: Chi-square, P: Probability calculated compared to $P_{0.05}$ = 3.84

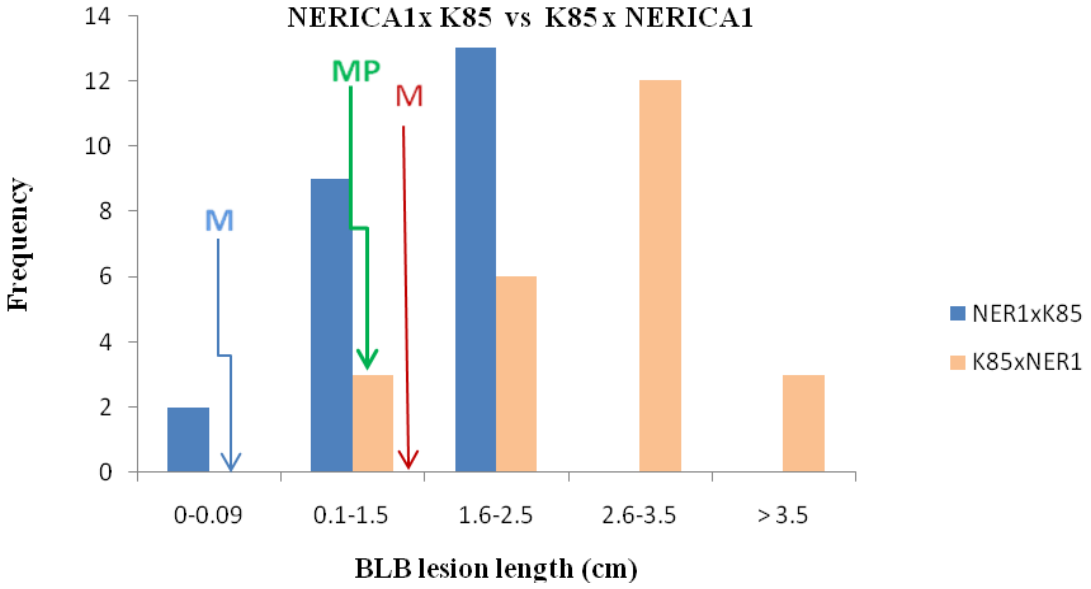

Figure 2 Frequency distribution for UGX20-2 in a cross NERICA1 x K85 and its reciprocal cross

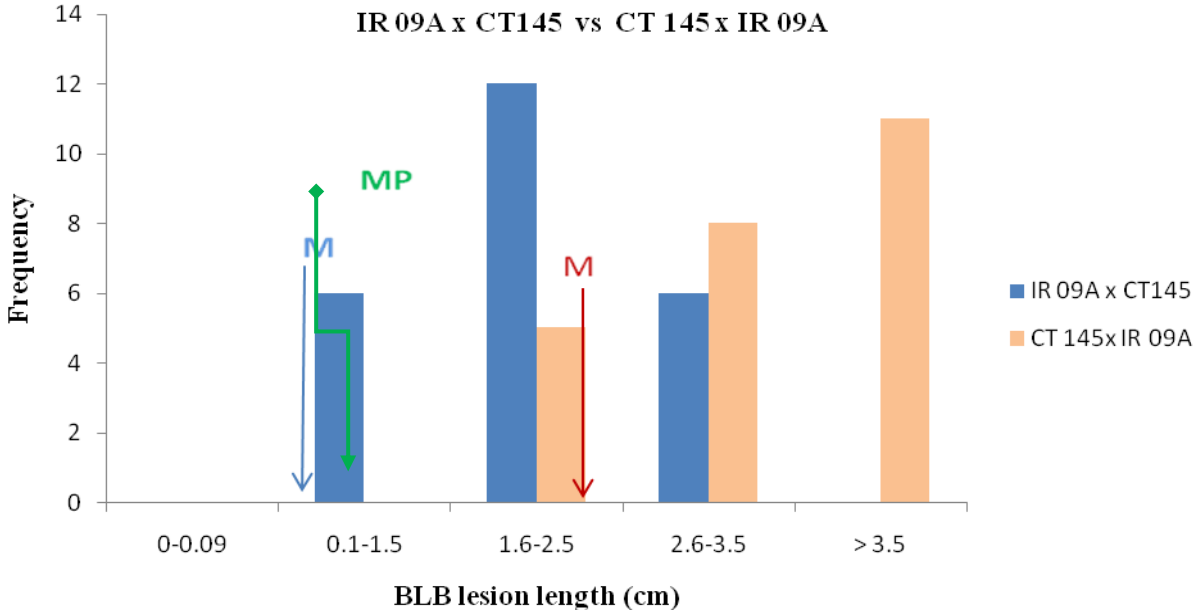

Figure 3 Frequency distribution for UGX20-2 severity in IR 09A x CT145 and its reciprocal cross

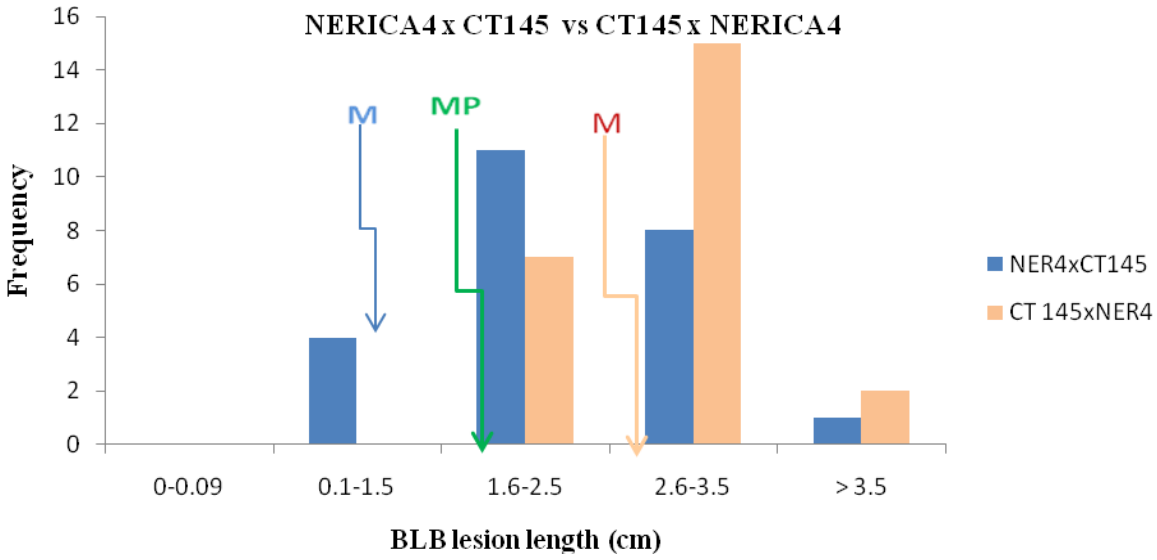

Figure 4 Frequency distribution for UGX20-2 severity cross NERICA4 x CT145 and reciprocal

3.2.2. Analysis of combining ability for resistance to the rice bacterial blight

The analysis of variance for resistance to bacterial blight revealed highly significant differences (P =0.001) among parents and F_2 progenies (Table 7).

Table 7 Mean squares of resistance for F2 progenies (with parents)to bacterial leaf blight

Source	df	MS	Fcal	Fprob
Rep	1	0.142	0.7785ns	0.385
Rep.Block	6	0.407	2.230ns	0.069
Genotypes	35	5.042	4.55***	9.908E-15
Residual	29	0.166	0.907	
Lattice Effective Error	29	0.183		

ns: non-significant; ***: significant at p = 0.001

3.2.3. Variance components and heritability estimates

Variance components and heritability estimates are summarized in Table 8. The results showed that SCA variance was smaller than that of etheir GCA variance. A high value was found for Baker's ratio (0.75). Narrow sense coefficient of genetic determination (NSCGD) was 57% and broad sense coefficient of genetic determination (BSCGD) was 77%.

Table 8 Mean squares of general and specific combining abilities and their ratios

Source	df	MS	Fcalc	Fprob	Var.Comp	EMS
GCA(R)	3	1.448	15.908	1.083E-06	0.144	σ2 e' + 9.4*σ2GCA(R)
GCA(S)	4	0.972	10.676	9.213E-06	0.082	σ2 e' + 10.75*σ2GCA(S)
SCA	18	0.198	2.170	2.434E-02	0.077	σ2 e' + 1.4*σ2SCA
Recipr	10	0.321	3.526	2.655E-03	0.230	σ2 e' + 2σ2Recip
Error	35	0.091			0.091	σ2e'
Baker's Ratio			0.75			
NS-CGD (Genotype mean basis)			0.57			
BS-CGD (Genotype mean basis)			0.77			

df: Degrees of freedom; MS: Means square; F: variance ratios; EMS: Expected means square; Var Comp: Variance components; GCA: General combining ability; SCA: Specific combining ability.

3.2.4. General Combining Ability (GCA) effects for parents

Results showed highly significant differences (P ≤ 001) for the non-adaptive (resistant) parents and high significant difference (P ≤ 0.01) for the adaptive parents. It also showed that the adapted parent IR24 reacted different from the other four parents against the UG20-2 isolate indicating that it is resistant as expected (Table 9).

Table 9 Estimation of General Combining Ability effects for bacterial blight resistance for parents

Parents	Status before evaluation	GCA effects
NERICA1	Resistant	-0.550***
NERICA 4	Resistant	-0.085ns
CT 12	Resistant	-0.705***
IR 09A	Resistant	-0.144ns
K85	Susceptible	0.234ns
K5	Susceptible	0.608***
GSR-I-0057	Susceptible	0.236ns
CT 145	Susceptible	0.469***
IR 24	Susceptible	-0.144ns

ns, = non-significant; *, **,***:= significant at p ≤ 0.05,p≤0.01 and p ≤ 0.001, respectively;

Negative GCA effects were shown by all resistant cultivars. On the other hand, all susceptible cultivars except IR 24 showed positive GCA effects. Of the resistant cultivars, CT12 (-0.71) and NERICA1 (-0.55) had the highest negative GCA effects. Similarly, the susceptible lines K5 (0.608) and CT 145 (0.469) had the highest positive GCA effects

3.2.5. Specific combining ability (SCA) and reciprocal effects

Both the specific combining ability (SCA) and reciprocal effects has showed significant differences at p ≤ 0.05 and p ≤ 0.01, respectively (Tables 10and 11).

Table 10 Estimation of Specific Combining Ability (SCA) effects

Parents	K 85	K 5	GSR-I-0057	CT 145	IR 24
NERICA1	**-0.078**	**-0.191**	**0.177**	**0.110**	–
NERICA 4	**-0.017**	-0.041	**0.130**	**0.026**	0.834
CT 12	–	**0.062**	-0.099	-0.268	–
IR 09A	0.374	-0.598	0.107	**-0.442**	**0.104**

–: missing cross; bolded-both direction present, normal for one direction only.

Table 11 Estimation of Reciprocal (REC) effects

Parents	K 85	K 5	GSR-I-0057	CT 145	IR 24
NERICA1	-0.312	-0.311	-0.568	-0.502	–
NERICA 4	-0.018	ϯ	-0.287	-0.694	ϯ
CT 12	–	-0.408	ψ	ψ	–
IR 09A	ψ	-0.598	ϯ	-0.322	-0.027

– ψ ϯ : missing cross, missing in the forward direction), missing in reverse direction

Among the crosses involving NERICA1 x K85, NERICA1 x K5, NERICA4 x K85, CT 12 x GSR-I-0057, CT12 x CT145, IR09A x K5 and IR09A x CT145 at least one parent had negative GCA effects. However, other crosses involving at least one similar parent, produced the progeny that exhibited positive SCA effects, namely NERICA1 x GSR-I-0057, NERICA1 x CT145, NERICA4 x GSR-I-0057 and CT12 x K5.

4. DISCUSSION OF THE RESULTS

4.1. Number and nature of genes controlling bacterial leaf blight

From this study it was evident that both dominant and epistatic genes were involved in conferring resistance to the BLB isolate UG 20-2 from Pallisa. This conclusion reflects to the segregating patterns observed in this study; 3:1, 13:3 and 15:1. The number and nature of genes involved in the inheritance of resistance to BLB were variable due to the complex genetic interactions between resistance genes and isolates. Depending on the genetic nature of the genotypes involved in a cross, the resistance could be conveyed by single dominant genes; two independent genes,- one recessive and one dominant, or two independent dominant genes. Though still unknown, these genes could be incorporated into improved local varieties through backcrossing to increase resistance to the local pathogenic races. Crosses that segregated in the ratio of 3:1 indicated that those are controlled by a single gene with a dominant effect, while those segregating according to the patterns 13:3 and 15:1 revealled epistatic gene action. Similar results were reported by Habururema et al. (2012) and Yoshimura *et al.* (1983).

4.2. Combining abilities

Both general and specific combining ability (GCA & SCA) effects were important in governing resistance to bacterial leaf blight disease (Tabien, 1989). Previous studies reported that, negative values for GCA effects are desirable in selecting superior parents for resistance to BLB (Kenga *et al.* 2004; Saleem *et al.* 2010, Hababurema, 2012). Based on these studies, the genotypes CT 12, NERICA1 and IR 09A were identified as potential sources of resistance to BLB. The predominance of GCA over SCA suggests that additive genetic effects are more important than non-additive in the inheritance of resistance for the genotypes under evaluation. This is shown by a variance component ratio (Baker's ratio) greater than 0.5 suggested that, a Baker's ratio equal to 1 would indicate total influence of additive genetic effects (Baker, 1978; Cravero *et al.* 2004).

In some results, Dabholkar (1992) classified heritability estimates in cultivated plants into categories of low (5 to 10%), medium (10 to 30%) and high heritability (30 to 60%). In the present study, the values of narrow sense coefficient of genetic determination (NSCGD) and broad sense coefficient of genetic determination (BSCGD) were very high (57% and 77%, respectively). It follows that resistance to bacterial blight in rice was much more heritable in the broad sense (H) than in the narrow sense (h^2) in this study and that the greater portion of heritable variation is additive in nature. The same results were reported by Tabien (1989), showing that, when four different Philippine races were tested on eight rice varieties, narrow sense heritability was high across races, ranging from 62% to 96%. The high Baker's ratio (0.75) and relatively high NSCGD in this trial indicate that the inheritance of BLB traits is controlled mostly by additive factors and can be used or detected in a later stage. This was also proven by the high significance shown in the reciprocal effects indicating the importance of the maternal contribution of the parents used during crossing. These reciprocal effects implies the importance of separately bulking the hybrids and their respective reciprocals and hence, of separately handling their respective progenies for selection in later generations. The extent of significance of the SCA shown in this experiment also indicated the presence of non-additive action leading to the possibility of selecting progenies at later filial generations.

5. CONCLUSIONS AND RECOMMANDATIONS

5.1. Conclusions

The research was conducted to seek out information on inheritance and gene action conditioning the transmission of resistance to bacterial leaf blight in selected rice genotypes. The information will contribute to the development of rice cultivars with durable resistance against prevailing races of the BLB pathogen in Uganda as well as all other countries in East Africa where the disease is threatening rice production. Results obtained, draws the following conclusions

1. The inheritance of resistance to rice bacterial leaf blight (BLB) could be interpreted qualitatively as arising from one of three patterns, depending on the parents involved in the F_2 segregating populations: by a single dominant gene inherited in a simple Mendelian manner, by two independent genes, one being recessive and the other dominant, or by two independent dominant genes. However, the nature of the F_2 distribution of BLB scores was generally continuous suggesting quantitative inheritance.
2. Analyzed as a quantitative trait both general combining ability (GCA) and specific combining ability (SCA) effects were important for resistance to BLB. Present study classified genotype IR24 among resistant lines, in agreement with results by Onasanya *et al.* (2009) opposing its universal suceptibility to Asian BLB isolates.
3. The significance of reciprocal effects for resistance to rice BLB emphasized the importance of the maternal contribution of the parents used in the hybridization. Further, a high contribution of reciprocal effects suggests the importance of separately handling the hybrids and their respective reciprocals for selection and makes critical the choice of the female parent for this trait.

5.2. Recommendations

1. This study identified sources of resistance to BLB disease in some rice cultivars including IR24, which in Asian rice populations is regarded as susceptible. It is recommended, therefore, to continue exploring possible BLB resistant sources of Ugandan germplasm in order to broaden the genetic base.
2. The local breeding program for resistance to BLB should focus on screening a wide range of genotypes and developing a resistant local check within the East Africa region or in Africa at large. The programme could also include germplasm from continental and international germplasm to achieve a greater genetic base for rice improvement in Uganda. The pathotype spectrum of the pathogen also needs to be considered when setting the breeding and testing strategy.

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